




Plant Nutrient Dynamics in Stressful Environments: Needs Interfere with Burdens

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1. Introduction

Several biotic and abiotic stresses influence plant growth, yield of agricultural crops, and the quality of plant products harvested for human or animal nutrition [1–6]. Abiotic stresses include nutrient starvation, unbalanced nutrient supply, and pollution, as well as climatic factors such as drought, flooding, heat waves, or low temperatures [7,8]. Climatic factors (especially extreme events) become more relevant in the course of global change, and may affect plant nutrition. Besides responses to individual stresses, combinations of stresses (e.g., drought and heat, drought and pests, drought, and unbalanced nutrient supply) must be borne in mind [5,9]. The severity of stresses and the timing of stress periods (phase of plant development, duration) are relevant for the impacts on various plant species or various varieties of a given species. Furthermore, recovery phases following stress periods must be also considered when evaluating stress impacts in a comprehensive manner [10]. This special issue addresses impacts of various stresses on plant nutrient acquisition, translocation, and accumulation in the harvested plant parts; however, only a limited number of stress impacts can be presented in detail.

2. Nutrient Availability and Acquisition

Liebig's law (initially focused on the availability of mineral macronutrients, and later also on micronutrients) was extended and integrated into a new concept presented in the review by Haneklaus et al. [5]. A balanced supply of macro- and micronutrients is essential to decrease the susceptibility of plants to biotic and abiotic stresses. Silicon—an element not belonging to the essential nutrients—plays a key role in the response of plants to biotic stresses (e.g., fungal attack) and a series of abiotic stresses such as drought or heavy metal stress [5,11–13]. For example, silicon can decrease the toxic effects of heavy metals or play a protective role against fungal diseases by positively influencing the structure and function of plant cell walls [5].

A research article contributed to this special issue by Bouranis et al. [14] addresses interactions between various nutrients and forms of nutrients with special reference to elemental sulfur and to iron in calcareous soils. Iron nutrition of crops can be improved by the addition of elemental sulfur to a standard fertilizer mixture. This was demonstrated for durum wheat on a calcareous soil. The addition of elemental sulfur lead to heavier vegetative plant parts and ears. Iron and organic sulfur contents were increased in all plant parts by this treatment, and yield quantity was also positively influenced. This paper nicely demonstrates the necessity to consider various aspects of plant nutrition in a broad

context, including plant/soil interactions, in order to optimize yield quantity and quality, as well as to decrease the susceptibility of plants to various stresses.

Interactions between magnesium supply and light levels with respect to photosynthetic efficiency were investigated by Dias et al. [15]. Experiments with coffee plants grown under controlled conditions provide evidence that optimized magnesium concentrations in the nutrient medium are important for maximal CO₂ assimilation rate, as well as for highest water use efficiency. Stomatal conductance depends on light and magnesium supply, illustrating the interaction between these two factors. Furthermore, increased magnesium concentrations in the nutrient solution led to increased magnesium and decreased potassium in leaf dry matter. Physiological processes (e.g., growth, photosynthesis, transpiration, seed filling) and the composition of collected plant material (e.g., hay, cereal grains) must be borne in mind when addressing aspects of plant nutrition in stressful environments.

The three papers mentioned above clearly illustrate the importance of addressing nutrient disorders in a broader context. Various stresses may affect nutrient acquisition by plants and their distribution within plants. In contrast, the nutritional status of plants is relevant for the responses to stresses. Appropriate fertilization is a key aspect, but fertilizers must be applied before or at the beginning of the main growth period when environmental conditions throughout this period and during the subsequent maturation phase cannot yet be known. As a consequence, plant growth, yield, and nutrient consumption may be negatively influenced, and deviate from average seasons. In such situations corrections in agronomic practices may become necessary during the following season(s). It remains a challenge to further integrate nutritional aspects and stress responses. In this context, it must be borne in mind that agricultural practices and the genotype spectrum available for crop production are permanently evolving, and may bring additional complexity to a comprehensive network of regulatory interactions.

3. Nutrient Redistribution within Plants and Accumulation in Harvested Plant Parts

Besides nutrient availability in soils, nutrient distribution and redistribution within the plant are important for the final contents of the various plant parts. Such transport processes and their regulation allow an accumulation of nutrients in harvested vegetative [16] or reproductive plant parts [17,18]. The mobility of an element or of certain forms of an element in the phloem is crucial for redistribution processes within the plant [13,19,20]. Such redistribution processes are crucial for heavy metal homeostasis [21], hyperaccumulation [22], and toxicity [11].

Possibilities to increase phosphorus use efficiency in wheat and *Arabidopsis* were reviewed by Kisko et al. [19]. The optimized use of phosphorus is highly relevant from an ecological (e.g., risk of eutrophication), as well as from an economical (e.g., fertilizer costs, quality of yield) point of view. Inorganic phosphate transport is emphasized in this review with respect to optimal use of phosphorus fertilizers and phosphorus contents in edible plant parts. A list of genes involved in sensing, uptake, transport, and signaling of inorganic phosphate in *Arabidopsis thaliana* and wheat documents the actual state of knowledge.

Biofortification is an important keyword in this context. Low zinc contents in plant products are a serious issue for human nutrition, and may cause zinc deficiency for a large percentage of the worldwide population [16,23]. Biofortification was, in the past, mainly investigated in staple crops (e.g., wheat, potato). The research article by White et al. [16] is focused on the zinc biofortification in leafy brassicas such as broccoli or cabbage. These plants, grown worldwide, are directly consumed by humans, and improved zinc contents in their leaves may help to provide sufficient zinc for the population in regions with inadequate zinc supplies. However, an excess of zinc can be phytotoxic. Therefore, there are limits for increasing zinc levels in collected plant parts without negatively influencing the plant itself. Based on these facts, zinc biofortification of leafy brassicas must be optimized, taking into account the zinc demands for human nutrition, as well as the possible toxic effects of elevated zinc on plant growth and/or metabolism [11,16,22].

4. Impact of Global Change on Plant Nutrient Dynamics

Global climate change with a string of extreme events (e.g., heat waves, droughts) cannot be ignored when addressing plant nutrient dynamics these days. The availability of nutrients in the soil, their acquisition, assimilation, distribution/redistribution within the plants, and the nutrient balance sheets for fields can be severely disturbed by climatic stress factors [13,24–27]. Such effects may not be restricted to the actual growing season, and may be relevant for the subsequent years(s).

Etienne et al. [13] contributed a review focused on senescence of vegetative plant parts and nutrient redistribution in annual crops. Drought effects on nutrient dynamics within the shoot, including remobilization from senescing leaves and transport to reproductive structures via xylem and phloem, are discussed in this paper. It must be assumed that the points addressed will become more relevant in the course of climate change, with predicted more frequent and/or more severe drought periods in many regions. Water fluxes, assimilatory activities, and the redistribution of inorganic nutrients and of assimilates are affected by this stress. The relative mobilities within plants vary between different macro- and micronutrients. Therefore, the drought effects on redistribution must be considered in an element-specific manner, avoiding unjustified generalizations. Nutrient deficiencies, or other stresses such as drought or heat, may influence the life span of leaves, as well as the composition of the harvest (e.g., grains) or of the stover.

The impact of drought on nitrogen, phosphorus, and potassium nutrition was investigated in young maize plants and documented in a research article by Studer et al. [25]. These three elements are frequently limiting, and represent classical fertilizer components. Changes in root and shoot growth, as documented with altered root/shoot ratios for dry matter, were identified as an important mechanism to improve stress tolerance in crops. In a broader context, structural responses to stresses may be as important as physiological changes to improve overall susceptibility [26–28]. Drought impact on symbiotic interactions, such as nitrogen fixation in legumes [29], or on mycorrhizal symbiosis [30], is a further important mechanism to influence the overall performance of crop plants.

5. Genetics and Breeding for Tolerant Crops

The elucidation of relevant genes and of genetic potentials are an important basis for breeding crop varieties with improved performance in stressful environments [31–35]. Besides traditional breeding programs, new tools to improve stress responses became available over recent decades, and may allow more direct genetic improvements to be made. Such programs could further improve well performing varieties when exposed to stresses.

Mastrodomenico et al. [31] started a research program in the corn belt based on old maize varieties (*expired plant variety protection germplasm*) and aimed at identifying possibilities of improving the performance under nitrogen stress (poor nitrogen availability). The paper is based on data from field experiments from four years at eight locations. Large numbers of inbreds (53 non-stiff, stalk synthetic and 36 stiff stalk synthetic) were included in this program to improve nitrogen-use efficiency. The authors present a perspective to identify the genetic potential, and to breed genotypes with a good overall performance under low nitrogen supply.

The research article by Chietera et al. [32] is also focused on nitrogen stress, and proposes new breeding targets including morphological and physiological properties. This research article is based on experiments with the hydroponically grown model plant *Arabidopsis thaliana*. A broad range of nitrate concentrations in the nutrient medium allowed us to undertake comprehensive analyses of four lines differing in their nitrate utilization properties. The findings were integrated into a statistical model predicting biomass production from nitrate supply. The article may serve as a basis for refining breeding programs for crops.

The possibilities of using all technologies available today—including genetic engineering tools—are presented in a comprehensive review by Roberts and Mattoo [33]. Sustainable intensification in agriculture to provide adequate food for an ever-growing worldwide population is a key aspect in this paper. The authors emphasize the challenge for the scientific community to provide the basis and

suitable techniques for breeding programs, taking into account changing environmental conditions (e.g., global change), potentials of changes in cropping systems, as well as biotic stress impacts in the future. Biotechnological approaches must be envisaged to provide cultivars with improved stress tolerance (abiotic and biotic stresses) [33].

6. Conclusions

The papers included in this special issue cover a broad range of aspects ranging from genetics and breeding to crop production in the field. Climate change, intensified agriculture, modifications of land use, or pollution are often accompanied by larger fluctuations including extreme events. The growing world's population and nutrient deficiencies in agricultural products for human or animal nutrition, or pollutants in harvested products in some regions (quality of yield), are important points to be integrated in a comprehensive analysis aimed at supporting agriculture on the way into a challenging future. It is therefore necessary to develop suitable models to identify potentials and risks. Instabilities (e.g., caused by climatic factors or pests) should be detected as early as possible to initiate corrections in the nutrient supply or in other growth conditions. Sensitive detection systems for nutrient disorders in the field can facilitate this task, and are therefore, highly desirable [36].

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